Journal of the Royal Society of Arts

NO. 4893 FRIDAY, 20TH FEBRUARY, 1953 VOL CI

FORTHCOMING MEETINGS

MONDAY, 23RD FEBRUARY, AT 6 p.m. The first of two CANTOR LECTURES on "*The Safety Factor in Construction*", by G. Anthony Gardner, O.B.E., M.I.Struct.E., Chief Structural Engineer, Ministry of Works. (The syllabus for these lectures, which will be illustrated with lantern slides, was published in the last issue of the *Journal* on 6th February.)

TUESDAY, 24TH FEBRUARY, AT 5.15 p.m. COMMONWEALTH SECTION. "*Tsetse Fly Control*", by K. R. S. Morris, B.Sc., lately Director of the Department of Tsetse Control, Gold Coast. J. W. Munro, C.B.E., M.A., D.Sc., Professor of Zoology and Applied Entomology, Imperial College of Science and Technology, will preside. (The paper will be illustrated with lantern slides. Tea will be served from 4.30 p.m.)

WEDNESDAY, 25TH FEBRUARY, AT 2.30 p.m. CADMAN MEMORIAL LECTURE. "*Improving Coal Production*", by E. H. Browne, C.B.E., M.A., Director-General of Production, National Coal Board. Major W. H. Cadman, M.B.E., B.Sc., F.R.I.C., will preside.

MONDAY, 2ND MARCH, AT 6 p.m. The second CANTOR LECTURE on "*The Safety Factor in Construction*", by F. C. Thompson, D.Met., M.Sc., Professor of Metallurgy, University of Manchester, and President-Elect, Institute of Metals. (The syllabus for this lecture, which will be illustrated with lantern slides, was published in the last issue of the *Journal* on 6th February.)

WEDNESDAY, 4TH MARCH, AT 2.30 p.m. "*The Assessment of Suitability for Employment*", by C. B. Frisby, Ph.D., B.Com., Director, National Institute of Industrial Psychology. D. W. Harding, M.A., Professor of Psychology in the University of London, will preside. (The paper will be illustrated by epidiascope.)

FRIDAY, 6TH MARCH, AT 7.30 p.m. FILM EVENING. (See special notice.)

WEDNESDAY, 11TH MARCH, AT 2.30 p.m. "*The High Paddington Scheme*", by Sergei Kadleigh, A.R.I.B.A. L. Dudley Stamp, C.B.E., D.Lit., D.Sc., Professor of Social Geography, London School of Economics and Political Science, will preside. (The paper will be illustrated with lantern slides.) An architectural model of the Scheme, which is a proposal to construct a town for 8,000 inhabitants over sidings outside Paddington Station, will be displayed in the Society's Library from Monday, March 9th, to the day of the meeting.

FILM EVENING

It is hoped to show on March 6th, at 7.30 p.m., the full version of the late Robert Flaherty's ***Louisiana Story***, a famous film which has hitherto seldom been seen in this country except with substantial cuts. Special assistance has been given to this end by Mrs. Flaherty and others, but the arrangement is still contingent upon the arrival of the film in this country before that date. Should the film not be available on March 6th, an alternative programme, which will include *Daybreak in Udi* (a dramatic film of social development in Nigeria) will be shown, and arrangements will be made to show *Louisiana Story* at a later date.

Fellows are entitled to introduce two guests, and light refreshments will be served in the Library afterwards at a charge of 1*s.* per head.

CORONATION CELEBRATIONS

The Council intends to arrange a social function for overseas Fellows visiting London for the Coronation, should there be sufficient numbers to justify holding it, and it would therefore be appreciated if those interested would kindly notify the Secretary as soon as possible.

MEETING OF COUNCIL

A meeting of Council was held on Monday, 9th February, 1953. Present: Mr. E. Munro Runtz (in the Chair); Mr. F. H. Andrews; Mr. A. C. Bossom; Sir Frank Brown; Sir Edward Crowe; Professor E. C. Dodds; Sir John Forsdyke; Mr. John Gloag; Sir Ernest Goodale; Mr. A. C. Hartley; Dame Caroline Haslett; Dr. R. W. Holland; Mr. F. A. Mercer; Mr. O. P. Milne; Sir William Ogg; Mr. E. M. Rich; Sir John Simonsen; Professor Dudley Stamp; Mr. William Will; Mr. J. G. Wilson; Sir John Woodhead, and Miss Anna Zinkeisen; with Mr. K. W. Luckhurst (Secretary) and Mr. R. V. C. Cleveland-Stevens (Assistant Secretary).

ELECTIONS

The following candidates were duly elected Fellows of the Society :

Abrahams, Arthur Lionel, London.
Adewusi, Mrs. Selina Ibifura, London.
Adeyi, Adebiyi Omowonuola, M.A., London.
Ali Nur, Abdel Salam, Edgware, Middx.
Björkstrand, Lars Einar Bernhard, Northwood, Middx.
Burton, Carlyle Archibald, B.A., Bridgetown, Barbados, B.W.I.
Cheung, Lee Iu, C.B.E., Kowloon, Hong Kong.
Clarke, Rodney Eyre, Bisley, Surrey.
Coulson, Douglas Joseph, M.A., Wem, Salop.
Eboh, Mrs. M. O., London.

Ellis, Cuthbert Hamilton, Brighton, Sussex.
Farrer, Keith Thomas Henry, M.Sc., Blackburn, Victoria, Australia.
Fuchs, Vivian Ernest, M.A., Ph.D., Cambridge.
Gregory, Francis, London.
Grindle, William George, London.
Heming, Jack Rupert Dempster, Richmond, Surrey.
Hockett, Robert Casad, M.A., Ph.D., New York, U.S.A.
Honour, Richard John William, Oxford.
Howe, Lyall Francis, Toorak, Victoria, Australia.
Ive, Oliver, M.R.C.S., L.R.C.P., London.
Johnson, Oscar Ernest, M.A., Great Gransden, Beds.
Le Mon, Edward Hugh, Cliftonville, Kent.
Lord, Cyril, A.M.C.T., London.
Luke of Pavenham, The Rt. Hon. Lord, T.D., D.L., J.P., Odell, Beds.
Lush, Brigadier Maurice Stanley, C.B., C.B.E., M.C., Tripoli, Libya.
Lyle, Thomas McElderry, C.S.I., C.I.E., Leixlip, Ireland.
MacLeod, Alexander Walker, Sheriff Hill, Co. Durham.
Maegraith, Peter, Sydney, N.S.W., Australia.
Manuel, Donaldo, B.A., LL.D., Pasadena, California, U.S.A.
Maycock, Arthur George, Salisbury, Southern Rhodesia.
McMullen, Rene A., London.
Mellor, John Hanson, Kidderminster, Worcs.
Morrell, George Frederick, Tunbridge Wells, Kent.
Rates, Roy Douglas, F.L.A., London.
Saha, Professor Nibaran Chandra, M.Sc., Ph.D., Aligarh, India.
Wallis, Captain Jack Raphael, M.C., Accra, Gold Coast.
Walmsley, Bernard, Wheelton, Lancs.

The following candidate was duly elected an Associate Member of the Society:

Harrison, Miss Gillian Evelyn Mary, Shepperton, Middx.

The following Colleges were admitted under Bye Law 66:

Grantham Technical College, Lincs.
Mid-Essex Technical College & School of Art, Chelmsford, Essex.

EXAMINATIONS COMMITTEE

Approval was given to certain revisions in the constitution and membership of the Examinations Committee.

ALBERT MEDAL FOR 1953

Preliminary consideration was given to the award of the Albert Medal for 1953.

BOARD OF ARCHITECTURAL EDUCATION OF THE ARCHITECTS REGISTRATION COUNCIL

Mr. O. P. Milne, F.R.I.B.A., was re-appointed as the Society's representative on the Board of Architectural Education of the Architects Registration Council.

LONDON SOCIETY

Professor A. E. Richardson was appointed the Council's representative on the Council of the London Society in succession to the late Lord Broughshane.

OTHER BUSINESS

A quantity of financial and other business was transacted.

MICROBIOLOGY

Three Cantor Lectures by

P. W. BRIAN, Sc.D.

of Imperial Chemical Industries Ltd.

I. GENERAL BACKGROUND

Monday, 17th November, 1952

Microbiology is the study of those small living creatures which we speak of collectively as micro-organisms. The justification of elevating the study of organisms primarily grouped together by their small size to the status of a distinct branch of science, is a topic I hope to take up again in a later lecture. To-day, I am going to try to provide the groundwork on which the two subsequent lectures will be based, by briefly discussing the main characteristics of micro-organisms, their structure, relationships, biochemical activities and their distribution.

In the course of our everyday life we are accustomed to distinguish two kinds of living organisms, plants and animals. You can all of you think of various reasons why plants are different from animals; animals move about, plants are stationary; animals ingest solid food, plants absorb it through all or part of their external surface; plants are green, animals may be any colour. None of these differences are absolute but the general distinction is there. Perhaps the most important of these differences is that relating to colour of plants, because this is associated with a basic difference in the nutrition of plants and animals. Chlorophyll, the green pigment characteristic of plants, enables them to use solar energy to reduce atmospheric carbon dioxide, carbon compounds produced in this way being used to synthesize all the numerous carbon-containing compounds of which the plant organism is composed. Animals, on the other hand, have to obtain their energy and carbon from pre-formed organic material; thus, in the final analysis, animal life depends on plant photosynthesis for the carbon compounds it requires. This distinction is biologically fundamental and, in the world of large organisms which we see around us, is fairly clear-cut. But even there, there are some organisms usually regarded as plants, such as the higher Fungi (mushrooms and toadstools), which lack chlorophyll and, like animals, need pre-formed organic carbon compounds. In the world of micro-organisms, as we shall see, the distinction between the plant mode of life (autotrophy) and the animal mode of life (heterotrophy) is equally important, though the dividing line between plant and animal is even less well-defined.

In addition to the familiar world of larger animals and plants, whose sizes can be measured in millimetres and centimetres, if not metres, there is a hidden world of micro-organisms, equally rich and varied in form, so small that even the millimetre is too large a measure. For these the unit of length is the *micron* (one thousandth of a millimetre), usually symbolized by the Greek letter μ.

The first glimpse into this unseen world was made nearly three hundred years ago by a draper of Leyden, Antonie van Leeuwenhoek. He made a simple microscope with which it was possible, in his hands at any rate, to see many kinds of micro-organism. In a series of letters to the Royal Society, of which he was a Fellow, he described "little animals" so vividly and accurately, in spite of his limited vocabulary and lack of familiarity with science in general, that they can be easily recognized to-day as Bacteria, Protozoa and Algæ, and even identified to genus or species. He found them in ponds, streams and canals; in water in the gutters round the roof of his house; in scrapings from his mouth and in the stomach of a shrimp; in organic infusions left to stand in the air.

After Leeuwenhoek, as microscopes were improved, knowledge of these micro-organisms increased rapidly so that by the middle of the nineteenth century much was known of their structure. But this work had been almost entirely descriptive and study of the life processes of micro-organisms was negligible until Pasteur began his investigations of fermentation. His paper of 1852—"Mémoire sur la fermentation dite lactique"—may be said to be the beginning of the modern science of microbiology, and in particular of that branch which we may call chemical microbiology, or microbial biochemistry.

But before we begin to consider the results of investigations of microbial biochemistry, I want to give you some idea of the great variety of things included under the term micro-organism. I want to make a special point of this because for various reasons it has come about that many people seem to think the words micro-organisms and bacteria are synonymous—a most misleading view. I shall begin with those most plant-like.

The *Green Algæ* are familiar to most of you as the slimy green growths one sees in ponds or on stones in streams, or as the green powdery material one sees on tree trunks. They may be unicellular organisms, small groups of cells, or simple filaments composed of cells placed end to end. Even in the most complex multicellular forms, in the vegetative stage all cells are to a great extent independent; there is little or no differentiation of function. Also belonging to this group are the diatoms, favourite objects of study to the microscopist for their beautiful shapes and the elegant sculpturing of their siliceous cell walls. Diatoms can often be found in fresh and sea waters and even in soil in tremendous numbers. Most of the Green Algæ are obviously plants. Typical forms contain chlorophyll, concentrated in special chloroplasts; they have cellulose cell-walls. But many are motile (e.g. *Chlamydomonas*), motility depending on special whip-like organs known as flagellæ, a form of locomotion very similar to that of some simple animals. Some of these unicellular motile forms, such as *Euglena*, have no cellulose cell-wall so that virtually their only plant-like character is the possession of chlorophyll in chloroplasts and the mode of nutrition associated with it.

A point to be noted here is that many of the more highly evolved multicellular forms, while possessing cell-walls and being non-motile in the vegetative phase, produce sexual reproductive cells which are motile and without a cell-wall. This is usually interpreted as indicating that the ancestry of the Green Algæ

lies in some simple motile form without cell-walls, the possession of cell-walls and the non-motile habit being characters developed in the course of evolution.

The *Fungi* are commonly regarded as plants, though that seems to me a matter of convention rather than an indication of real relationship with the chlorophyll-containing plants: there is no evidence whatsoever that any ancestors of the Fungi as we know them contained chlorophyll. The typical vegetative form to be found in the Fungi is thread-like—the hypha. This has a cell-wall based on cellulose in one small group of Fungi, on chitin, a structural element known otherwise only in animals, in most Fungi. This thread or tube may or may not be divided into cells by cross septa. Even the largest and most elaborate Fungi, such as toadstools or the bracket fungi, are made up of masses of interweaving hyphæ. There are some non-filamentous, single-celled Fungi, notably the yeasts. The yeasts, of the greatest possible interest and importance biochemically, are almost certainly derived from filamentous Fungi; in this case the unicellular habit is not a primitive character, but a case of reversion. Some Fungi have motile sexual cells, again suggesting an origin from motile organisms. No Fungi contain chlorophyll and, like animals, they have to be supplied with organic carbon.

The *Protozoa* include those micro-organisms which seem most animal-like and indeed are claimed as such by the zoologists. They are nearly all motile. Many ingest particles of solid food. Most are unicellular; some live as colonies of independent cells; others are perhaps better regarded as non-cellular in that, although there is no division into cells there is considerable differentiation of function within the cell. They include ciliates (e.g. *Paramecium*), common in contaminated water; these are actively motile forms with a high degree of organization, moving by the rhythmic beating of large numbers of motile hairs called cilia. They include the amœbæ; in their simplest form these are naked masses of protoplasm moving by a sort of mass flow of the cytoplasm. Some Protozoans are parasites in animals. Some form highly elaborate siliceous or calcareous skeletons. A group of organisms of this kind, of great abundance in sea water, are the *Foraminifera*. These normally live in the surface layers of sea water; their calcareous skeletons fall to the bottom of the sea where they form great depths of mud. This may in due course become fossilized, forming the rock familiar to us all as chalk. Finally, perhaps the most primitive group of Protozoa are flagellated forms similar in every way to such flagellate Algæ as *Euglena* except that they contain no chlorophyll.

We are now coming to a point I foreshadowed earlier, that among micro-organisms it becomes difficult to distinguish plant from animal. There is this large group of micro-organisms, which we call flagellates, consisting of a spherical or fusiform body, delimited by an elastic membrane but possessing no cell-wall, actively motile by means of its flagellæ. Some contain chlorophyll in chloroplasts and might be considered plant-like; these are claimed by the botanist as Algæ. Others may contain the plastids but no chlorophyll. Others may contain neither chlorophyll nor plastids but be identical in every other way to the plant-like forms, but are claimed by the zoologist as Protozoa. Furthermore, some of the

green forms which will assimilate carbon dioxide in the light, like typical plants, will live indefinitely in darkness if supplied with a suitable organic carbon source, losing their chlorophyll in the process. We can regard these flagellates as a primitive stock, where the differentiation into plant or animal modes of existence is just beginning: from this stock, or something very like it, the Algæ, Fungi and Protozoa have arisen during the course of evolution.

But we must continue with our survey. There remain two further groups of micro-organisms which do not seem to be at all closely related to those so far mentioned. Most important of these are the *Bacteria*. They are in general rather smaller than the micro-organisms so far discussed. They may be spherical (cocci), rod-shaped or spiral in form. They may be aggregated into filaments, as in the important sub-group *Actinomycetes*. They may or may not be motile. They may be colourless or pigmented. Most of them require to be supplied with an organic carbon source but there are exceptions to this, which I shall mention later. In the past it has been said that, unlike the other micro-organisms which we have considered, they possess no well-defined nucleus; recent research suggests that this is not so. They have usually been regarded as unicellular in most cases but recent research suggests that a simple multicellular structure is not uncommon.

Finally, there are the *Blue-Green Algæ* or *Cyanophyceæ*. These may be unicellular or filamentous. They are non-motile in the sense that no flagellate or ciliate stages are known. They contain chlorophyll, but this appears to be distributed throughout the cell, not in special organs (chloroplasts) as in the Green Algæ. It seems unlikely that they are related to the Green Algæ; morphologically and biochemically they show affinities to the bacteria.

These five groups of micro-organisms comprise the subject matter of these lectures. I shall not be able to deal with all groups equally because they have received most unequal study; for various reasons Bacteria have been studied much more intensively than the other groups and it is inevitable that I too shall have most to say about some of them. I want now to devote the rest of my time to-day to a brief discussion of some general aspects of the metabolism and distribution of micro-organisms.

Perhaps the most important thing one can know about the life of any organism is the kind of food it needs, because unless its nutrient requirements are satisfied no other life-processes are possible. I propose therefore to consider next the nutrition of micro-organisms. Their life, like ours, is based on the synthesis of all the complex molecules of which they are built, from simpler constituents. A supply of energy is needed if these syntheses are to proceed. First let us consider the supply of energy and, after that, the raw materials needed for biosynthesis.

Those micro-organisms (Green Algæ and Blue-Green Algæ) containing chlorophyll can trap some of the radiant energy of the sun and use it to reduce atmospheric carbon dioxide by the following reaction:

$$CO_2 + H_2O \xrightarrow{\text{light}} (CH_2O) + O_2$$

where (CH_2O) is the first product of photosynthesis. The nature of this first product is uncertain but a usual result of photosynthesis is accumulation of carbohydrate of molecular formula $(CH_2O)_n$. The energy stored in this carbohydrate can be drawn upon subsequently by a process of oxidation.

This form of photosynthesis, the only form known in higher plants, is not the only one known to micro-organisms. There are, for instance, a number of pigmented Bacteria which can reduce carbon dioxide in light if sulphide is present. Such conditions often occur in the mud at the bottom of shallow fresh or salt water. The so-called purple sulphur bacteria (*Thiorhodaceæ*) in the presence of light reduce carbon dioxide as follows:

$$2CO_2 + H_2S + 2H_2O \xrightarrow{\text{light}} 2(CH_2O) + H_2SO_4$$

This overall reaction proceeds in two steps. In the first the sulphide is oxidized only to the stage of sulphur; this is deposited *inside* the bacterial cell:

$$CO_2 + 2H_2S \xrightarrow{\text{light}} (CH_2O) + H_2O + 2S$$

In the second stage, which only occurs if no further sulphide is present, the intracellular sulphur is still further oxidized to sulphate:

$$3CO_2 + 2S + 8H_2O \xrightarrow{\text{light}} 3(CH_2O) + 3H_2O + 2H_2SO_4$$

In the reduction of carbon dioxide by the green sulphur bacteria (*Chlorobacteriaceæ*) the sulphide is reduced only to the stage of elemental sulphur, which is deposited *outside* the cell:

$$CO_2 + 2H_2S \xrightarrow{\text{light}} (CH_2O) + H_2O + 2S$$

Some of these bacteria can oxidize up to four times their weight of hydrogen sulphide daily.

Yet another variant is provided by the purple (non-sulphur) bacteria (*Athiorhodacea*) which can reduce carbon dioxide in the presence of light either in the presence of hydrogen:

$$CO_2 + 2H_2 \xrightarrow{\text{ght}} (CH_2O) + H_2O$$

or in the presence of a suitable fatty acid:

$$CO_2 + CH_3.CH_2.CH_2.COOH + H_2O \xrightarrow{\text{light}} 5(CH_2O)$$

I should like you to note three points about these variations on the theme of photosynthesis. First, that only in the case of that carried out by chlorophyll-containing plants does molecular oxygen appear as an end-product. Secondly, that the organisms obtaining energy by reducing carbon dioxide with sulphide can do so, and grow and multiply vigorously, only in the light and *in the absence of oxygen*; some of them can grow in the dark if oxygen and an organic carbon source are supplied. Thirdly, that all these means of reducing carbon dioxide can be regarded as a transfer of hydrogen from a suitable hydrogen-donor and that they can all therefore be regarded as variants of the following general reaction:

$$CO_2 + 2H_2A \xrightarrow{\text{light}} (CH_2O) + H_2O + 2A$$

There is some reason to believe that in micro-organisms the photosynthetic mechanism is still in a somewhat primitive and flexible state; some chlorophyll-containing Green Algæ (e.g. *Scenedesmus*) normally photosynthesize by the usual reaction:

$$CO_2 + H_2O \xrightarrow{\text{light}} (CH_2O) + O_2$$

but are able, in the presence of hydrogen, to reduce carbon dioxide without production of oxygen:

$$CO_2 + 2H_2 \xrightarrow{\text{light}} (CH_2O) + H_2O$$

and it has been claimed that some diatoms and Blue-Green Algæ can reduce carbon dioxide with hydrogen sulphide as the hydrogen-donor in a manner reminiscent of the purple sulphur bacteria. Photosynthesis, then, is a very much more variable phenomenon in micro-organisms than in higher plants.

Let us now turn to other methods of obtaining energy. You and I obtain energy by oxidation of part of our food, or, in starvation, of part of our body tissues. Some substances yield more energy on oxidation than others, and all of us know nowadays that carbohydrates and fats are calorific foods *par excellence*. Oxidation of glucose, ignoring the many steps involved, can be regarded as taking the following course:

$$C_6H_{12}O_6 + 6O_2 \longrightarrow 6CO_2 + 6H_2O + 686{,}000 \text{ calories}$$

This process of dissimilation, known as respiration, is *ærobic:* in other words molecular oxygen is an essential part of the reaction. Provision of energy by ærobic respiration is characteristic of most Fungi, Bacteria and Protozoa; it also takes place in the chlorophyll-containing Green Algæ and Blue-Green Algæ *in the dark*. (I should make it clear that higher plants and many of the Algæ cannot indefinitely carry on in this way; some of the more primitive Algae can, however, losing their chlorophyll in the process.) But many micro-organisms, especially the Bacteria, can provide themselves with sufficient energy by dissimilations not involving the intervention of molecular oxygen. Such oxidations lead to the accumulation of incompletely oxidized carbon compounds, such as ethyl alcohol:

$$C_6H_{12}O_6 \longrightarrow 2C_2H_5OH + 2CO_2 + 50{,}000 \text{ calories}$$

and this process is usually known as fermentation, a term which unfortunately has other meanings. The energy yield is much less than in ærobic respiration. Many Bacteria can grow indefinitely in the absence of oxygen or at low oxygen tension on the basis of energy acquired in this way. Other micro-organisms, moulds for instance, can carry out vigorous fermentations of this kind in the absence of oxygen but usually are unable to make much growth and eventually die unless oxygen is admitted. This faculty for anærobic existence and even vigorous growth is only found in micro-organisms and such micro-organisms are able to exist in habitats unsuitable for any higher organisms. Some Bacteria have carried this process to such a stage that they cannot live in the presence of oxygen; they are obligatory anærobes. Species of *Clostridium*, for instance, one

of which causes gas-gangrene in infected wounds, need complete anærobiosis for growth and apparently provide all their necessary energy by oxidation of amino-acids, an oxidation in which another amino-acid is the hydrogen-acceptor. One amino-acid is de-aminated and oxidized (providing the energy) and the other is de-aminated and reduced, giving an overall reaction:

$$R_1CH.NH_2.COOH + R_2.CHNH_2.COOH + H_2O \longrightarrow R_1.CO.COOH + R_2.CH_2.COOH + 2NH_3 + \text{cals.}$$

This is a highly specialized but not very efficient way of providing energy; the *Clostridia* are highly specialized in their nutrition in other ways, as their powers of synthesis are much reduced.

We have now discussed two main methods of obtaining energy, the photosynthetic method of using radiant energy from the sun, and the release of energy by ærobic or anærobic oxidation of organic materials. This does not exhaust all the possibilities known to micro-organisms. There are a number of Bacteria, some, as we shall see in a later lecture, of enormous natural importance, which derive their energy from oxidation of inorganic materials.

There are Bacteria which oxidize ammonia to nitrate. Species of *Nitrosomonas* oxidize ammonia to nitrite:

$$2NH_3 + 3O_2 \longrightarrow 2HNO_2 + 2H_2O + 158{,}000 \text{ calories}$$

and species of *Nitrobacter* oxidize the nitrite to nitrate:

$$2HNO_2 + O_2 \longrightarrow 2HNO_3 + 43{,}200 \text{ calories}$$

There are Bacteria capable of oxidizing various reduced sulphur compounds to elemental sulphur or sulphate. *Beggiatoa*, an organism usually considered to belong to the Bacteria but closely related in many respects to the Blue-Green Algæ, obtains energy by the following reaction:

$$2H_2S + O_2 \longrightarrow 2H_2O + 2S + 65{,}000 \text{ calories}$$

Thiobacillus thioparus can oxidize various reduced sulphur compounds; thiosulphate is oxidized by the following reaction:

$$5Na_2S_2O_3 + H_2O + 4O_2 \longrightarrow 5Na_2SO_4 + H_2SO_4 + 4S + 500{,}300 \text{ calories}$$

Thiobacillus denitrificans can oxidize sulphur with simultaneous reduction of nitrate :

$$5S + 6KNO_3 + 2CaCO_3 \longrightarrow 3K_2SO_4 + 2CaSO_4 + 2CO_2 + 3N_2 + 600{,}000 \text{ calories}$$

Thiobacillus thiooxidans also oxidizes sulphur:

$$2S + 3O_2 + 2H_2O \longrightarrow 2H_2SO_4 + 141{,}800 \text{ calories}$$

Of these organisms, the species of *Thiobacillus* at least are strictly ærobic organisms, and obligatorily autotrophic.

There is a group of Bacteria, known as iron-bacteria, which can obtain energy from oxidation of ferrous iron to ferric iron:

$$4FeCO_3 + O_2 + 6H_2O \longrightarrow 4Fe(OH)_3 + 4CO_2 + 81{,}000 \text{ calories}$$

These organisms are often seen making a reddish brown slime at the bottom of ditches in districts where the water contains iron salts. Yet other Bacteria obtain energy by oxidizing such unlikely substances as hydrogen, carbon-monoxide and methane.

So much for the extraordinary variety of means by which micro-organisms provide themselves with the energy necessary for synthesis. We will turn now to their other nutrient requirements. Many have very simple requirements. The photosynthetic Algæ in general need only inorganic salts: nitrogen in the form of nitrate or ammonia, phosphate, sulphate, potassium, magnesium and small quantities of a few other metals, such as iron, copper, manganese, zinc and molybdenum. Many Bacteria and Fungi need, besides their organic carbon source, only these same simple salts. A distinction can be made between those that are able to utilize nitrogen and sulphur in the completely oxidized form in which they most commonly occur in nature (i.e. nitrate and sulphate) and those that require more reduced forms. Thus many Bacteria and some Fungi are unable to reduce nitrate nitrogen and require ammonia nitrogen. Some Fungi have lost the power to reduce sulphate and require more reduced sulphur compounds.

Many micro-organisms, on the other hand, have more complex requirements. There appears to have been a definite tendency in evolution to lose certain powers of synthesis, notably of those constituents of enzyme complexes which we call vitamins, and of amino-acids. This tendency is seen in all groups, though less in the photosynthetic forms. Thus some Algæ, many Fungi, many Bacteria and most Protozoa require such vitamins as aneurin (B_1) and biotin for proper growth. Some Fungi, many Bacteria and many Protozoa have to be supplied with one or more amino-acids, which they are unable to synthesize themselves. This trend towards loss of synthetic function is carried to the greatest extremes in parasitic forms. Bacteria, Protozoa and Fungi afford many examples of specialized parasites on animals or plants and in many cases their nutrient requirements are exceedingly complex and, indeed, in many cases they have not yet been cultivated apart from their hosts. Many of the Protozoa normally ingest solid food—Bacteria, Algæ and other small organisms. In some cases it has been found possible to cultivate them in appropriate solutions without solid food; in other cases they can be grown with dead bacteria as their food; in some cases, as far as we know at present, live food is essential, indicating very complex requirements.

Before leaving this survey of the nutrition of micro-organisms, one further process unique to micro-organisms must be mentioned. That is nitrogen-fixation. The majority of micro-organisms have to be supplied with nitrogen, essential for the synthesis of protein, as nitrate, ammonia, amino-acid or even more complex organic forms. A few Bacteria and a few Blue-Green Algæ, which as I previously mentioned are apparently related to the Bacteria in many ways, are able to fix atmospheric nitrogen. There are species of Bacteria living free in most soils which do this; other species live symbiotically in the roots of plants, particularly leguminous plants, forming organs known as root nodules, where nitrogen is fixed, to the advantage of the plant partner of the symbiosis. In some water-logged tropical soils, such as paddy fields, nitrogen-fixation by Blue-Green

Algæ assumes importance. The mechanism of nitrogen-fixation is incompletely understood at present but the importance of the reaction to agriculture is undoubted.

This great range of different nutrient requirements can be reduced to a fairly simple scheme (see Table 1).

TABLE I

Source of energy	Requiring mineral sources of N, P, S and metals only			Requiring in addition one or more vitamins, amino-acids, and or other growth-factors
	N-fixing	Nitrate-N	Requiring reduced forms of N or S	
Light	Some Blue-Green Algæ	Most Green Algæ Blue-Green Algæ Purple (non-sulphur) Bacteria	Some Algæ and Blue-Green Algæ Green and Purple sulphur Bacteria	A few Green Algæ
Oxidation of inorganic substances		Iron Bacteria Some sulphate reducing Bacteria Nitrifying Bacteria	Some sulphate reducing Bacteria (e.g. *Thiobacillus thioparus*)	
Oxidation of organic substances	Nitrogen-fixing Bacteria	Some Fungi Some Bacteria	Some Fungi Some Bacteria	Some Fungi Some Bacteria Protozoa

Having dealt in very general terms with the basic nutrient requirements of micro-organisms we can now consider their distribution. It will be clear from what we have learnt already that many can live in an almost purely inorganic

medium whereas others will require much more specialized habitats with a supply of many complex nutrients.

Without doubt the most important habitats, both from the point of view of variety of species to be found and in numbers of organisms involved, are surface soils and surface waters. There are certain difficulties involved in counting numbers of micro-organisms but the sort of numbers one commonly finds in a gram of a surface soil are

Bacteria	1–100 millions
Actinomycetes	1–10 millions
Protozoa	100,000–1 million
Fungi	50,000–1 million
Algæ (Green and Blue-Green)	10,000–50,000

At times much higher numbers are found and there is reason to believe that most techniques seriously underestimate the numbers present. Micro-organisms are not uniformly distributed through soil. They are greatest in number near the surface; this of course applies particularly to Algæ, which need light for photosynthesis. But even at great depths some organisms, able to live in very low oxygen tensions, can usually be found. Micro-organisms are also concentrated near particles of decomposable matter and in the immediate vicinity of plant roots. There is, in fact, a mantle of micro-organisms completely surrounding plant roots under natural conditions; this zone of high microbial activity is spoken of as the rhizosphere.

The distribution of micro-organisms in the sea is somewhat different. In surface waters one finds great numbers of small Algæ, mainly diatoms; a population of hundreds if not thousands in each millilitre of water being not uncommon. Naturally enough these are concentrated in those layers of the sea to which sufficient light can penetrate (*circa* 80 metres depth in temperate zones) and numbers fall sharply below that limit. In more or less this same zone large populations of small animals develop. Among these animals are numerous Protozoa, notably *Foraminifera*, whose numbers may be of the same order as the planktonic Algæ. Bacteria, whose numbers depend to a great extent on the availability of decomposable animal or vegetable organic matter, are found in the same surface zone, perhaps greater in numbers towards the bottom of the zone, falling off in numbers gradually below that, but increasing tremendously in numbers in the ooze on the sea floor. Typical numbers of Bacteria (per ml. water or bottom ooze) observed are:

Depth (Metres)	*Numbers*
1	100–300
10	200–400
20	300–600
50	100–600
100	10–50
200	0–3
500	0–2
Bottom ...	1 million–16 millions

Most of the Bacteria in the bottom deposits, almost the only micro-organisms to be found there, are anærobes. Fungi are not as characteristic a feature of the microflora of the sea as they are of the microflora of soil, but fungal parasites of planktonic Algæ and Protozoa are more common than is generally supposed. The distribution of micro-organisms in fresh water is somewhat similar.

Soil and water, then, are the main primary habitats of micro-organisms. Much greater concentrations can be found in sewage systems, decomposing foodstuffs, and manure heaps, but such habitats can be considered to be secondary and dependent on human activity.

Another important habitat for micro-organisms is in the tissues of larger plants and animals. For various reasons this is the habitat that occurs first to most people, and it is these parasitic micro-organisms which have received most detailed study. The parasitic habit has been adopted by representatives of all groups of micro-organisms except possibly the Blue-Green Algæ. Bacteria are common causes of disease of man and animals, less frequently they are parasites of plants. Protozoa of various kinds are important parasites of man and animals; such diseases as malaria and trypanasomiasis are both caused by Protozoan parasites. Fungi are frequently parasitic on plants and to a more limited extent on animals also. A very few Green Algæ are parasitic on plants. A form of association between micro-organisms and plants or animals, more correctly termed symbiosis or commensalism, is also widespread, ranging from the mycorrhizal association between certain Fungi and tree-roots to the characteristic association of micro-organisms found in the digestive tract of many animals, above all in the rumen of ruminants.

Finally, there is the air around us. Almost all kinds of micro-organism are to be found in air, even at great heights, even at polar latitudes. In most cases they are only there in a resting state, awaiting deposition in some more suitable substratum before commencing growth. There is some suspicion, however, that some Bacteria may increase in numbers while air-borne.

This concludes my brief survey of the habitats in which micro-organisms can be found. I think I have made it clear that in my view the most important habitats are soil and water. There, micro-organisms often live in very crowded communities. I should like to dwell for a moment or two on the reason for this. Micro-organisms are able to exploit changes in their environment very much more rapidly than higher animals or plants, or, to put it in another way, they are in many ways much more dependent on their environment. Consider what happens when a piece of dead plant or animal tissue falls on the soil. The sudden access of foodstuffs stimulates saprophytic micro-organisms in its vicinity to very rapid growth, though until then they may have been in a state of suspended animation. With growth comes reproduction. Since reproduction in micro-organisms frequently only entails a simple division of the organism into two or more parts, it is not surprising that the process is much more rapid than in higher animals or plants. In fact, *Bacterium coli*, growing in a rich medium such as hydrolyzed casein, can divide once every ten or fifteen minutes. At this rate one organism can give rise to over one million organisms in five hours if the food

supply is sufficient. You will not be surprised therefore to find very high populations of micro-organisms in suitable situations and correspondingly great fluctuations in number as environmental conditions change.

Associated with this power of rapid multiplication goes a power of producing rapid chemical change. However small may be the changes produced by a single micro-organism, great changes can be produced by the combined activity of millions of millions. A further characteristic of the life of micro-organisms is of importance here. They are organisms of small mass but of very high surface area in relation to that mass. Because of this they usually need little in the way of special digestive apparatus; foodstuffs can pass into the organism by simple diffusion quite rapidly enough. But however great an advantage this may be, it brings with it what may sometimes be a disadvantage, at other times an advantage—that substances can readily diffuse out as well. The result is that metabolites are constantly leaking out, particularly, of course, those that are more water-soluble. A higher animal has its chemical interchanges with its environment highly controlled; food is taken in and, by and large, all that goes out is water vapour from the general surface, carbon dioxide from the lungs, and such other material as is periodically excreted in urine and fæces. All the manifold changes going on in the body are to a great extent part of the "private life" of the higher animal. Not so with the micro-organism, it has relatively little private chemical life; the chemical processes essential to its life are to a great extent immediately reflected in chemical changes in its environment. Of the substances diffusing out of its body are many, such as vitamins, enzymes and antibiotics, of "high biological activity", that is, likely to cause great changes in the life of other micro-organisms in its vicinity. This makes the study of relationships in mixed microbiological communities, such as soil and water, peculiarly fascinating.

II. NATURAL ACTIVITIES OF MICRO-ORGANISMS

Monday, 24th November, 1952

I am going to discuss to-day a few aspects of microbiological activity under natural conditions, so that you can form some estimate of the importance of micro-organisms in the economy of nature. First, we will consider the inter-relations between the carbon and nitrogen metabolism of micro-organisms and that of higher animals and plants.

I have already reminded you that all the organic carbon compounds in living beings, whether plant or animal, whether micro-organism or larger organism, derive ultimately from atmospheric carbon dioxide, fixed in photosynthesis. All animal carbon is derived from plant carbon. It is interesting to construct a flow sheet showing the paths of interchange between atmospheric carbon dioxide and the various kinds of living matter. This is done in Figure 1. In this

flow-sheet it is not possible to separate micro-organisms from other organisms rigidly. Instead three groups of living organism are shown occupying rather different places in the carbon chain. These are (a) "animals", including not only larger multicellular animals but also those micro-organisms, notably Protozoa, which ingest solid food; (b) "plants", which include all chlorophyll-containing organisms, i.e. Green Algæ, Blue-Green Algæ and photosynthetic Bacteria, as well as larger plants; (c) "micro-organisms" living a parasitic or saprophytic existence, Fungi and Bacteria being of special prominence here.

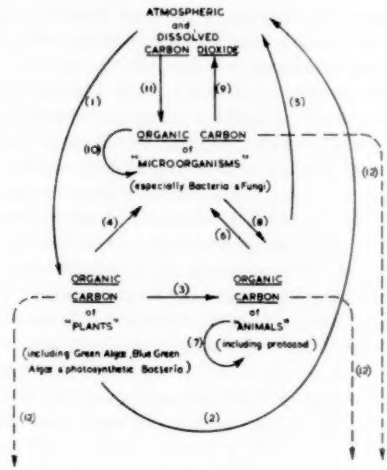

Figure 1

By far the most important path of carbon dioxide fixation is in photosynthesis by chlorophyll-containing plants (path 1 in Figure 1). This is the primary step of carbon accumulation. There are three main fates for this plant carbon: (*a*) part is returned directly to the atmosphere as carbon dioxide in respiration by the plant or in the respiration of micro-organisms parasitic on the plant or engaged in decomposition of the plant after death (path 2); (*b*) part becomes food for animals and is incorporated in the animal body (path 3); (*c*) part becomes incorporated in parasitic or saprophytic micro-organisms (Fungi and Bacteria) (path 4). The animal carbon has three possible fates, reappearance as carbon dioxide by respiration of the animal or of micro-organisms living upon it before or after death (path 5), incorporation in the bodies of Fungi or Bacteria (path 6) or it may reappear in the bodies of other, carnivorous animals (path 7). The organic carbon of the saprophytic Fungi and Bacteria and other micro-organisms which have not been considered to be "plants" or "animals" may either become the food of micro-organism-devouring animals, notably Protozoa (path 8), or

will return as carbon dioxide to the atmosphere in respiration or decay after death (path 9), or may be assimilated by other micro-organisms (path 10) before complete oxidation to carbon dioxide has taken place. To complete the picture, path 11 represents assimilation of carbon dioxide by those bacteria deriving energy from oxidation of inorganic materials, probably a very minor path of carbon accumulation.

To forestall any criticism for errors of omission I must mention here a recent biochemical discovery of some importance. Apparently many, if not all, organisms are capable of and usually do fix some atmospheric carbon dioxide heterotrophically, i.e. by using energy derived from oxidative breakdown of organic carbon compounds within the cell. Since this process does not result in a net increase of cell carbon I have omitted it from this flowsheet, in spite of its great intrinsic biochemical interest.

Some of these processes in the carbon cycle are rapid (e.g. carbon dioxide assimilation) and others are slow. An example of the latter is the decomposition of lignified plant residues, which resist microbial attack and only reappear as carbon dioxide after a considerable interval. Indeed, under certain conditions organic matter may become fossilized (path 12) in the form of peat, coal or petroleum, and this carbon does not return to the atmosphere as carbon dioxide for geologically considerable periods and, indeed, has only commenced to do so with any rapidity as a result of its increasing use by man as a source of energy.

My purpose is to assess the importance of micro-organisms in this carbon cycle. It can already be seen that they intervene in most of the main paths of carbon metabolism and play an important part in the eventual return of plant and animal carbon to the atmosphere as carbon dioxide. That is, they have an important dissimilatory role. They have also an important place in carbon assimilation, larger than is frequently realized. Carbon assimilation by land plants, that is mainly by higher plants (Angiosperms), can usefully be separated from that taking place in the oceans, that is mainly by diatoms and other microscopic Green Algæ. Rabinowitch has recently made some interesting estimates of the total yield of photosynthesis by these two groups:

	Area (millions of km^2)	*Average yearly carbon fixation* (tons per hectare)	*Total yearly carbon fixation* (millions of tons)
Oceans ...	361	3·75	155,000
Land ...	149	1·3	19,000

Thus carbon fixation in the oceans, predominantly by micro-organisms (Green Algæ), is eight times that of all land plants and the efficiency of fixation per unit area is considerably higher in the oceans. The magnitude of carbon turn-over attributable to microbial activity is most striking, when compared, for instance, with an annual world steel production of about 100 million tons.

Now let us turn to nitrogen metabolism, considering first the cycle as it takes place on land, i.e. on and in the soil. The flowsheet is diagrammatically presented in Figure 2. In this flowsheet micro-organisms of all kinds can be kept separate

from higher animals and higher green plants. You will see that for part of the cycle the nitrogen is mainly in organic combination as protein and for part it exists in inorganic form.

It is convenient to start with plants and animals. Animals depend ultimately on green plants for their protein-nitrogen (path 1), though, of course, in many cases the dependence is indirect since many animals are carnivorous (path 2). Only part of the plant protein produced is transformed to animal protein; on death, microbial action results in part of the plant protein appearing as protein in micro-organisms (path 3) and part appears as ammonia as a result of de-amination of amino-acids by micro-organisms during decomposition (path 4). Animal protein and the nitrogen in animal excreta also reappear as microbial protein or ammonia (paths 3a and 4a).

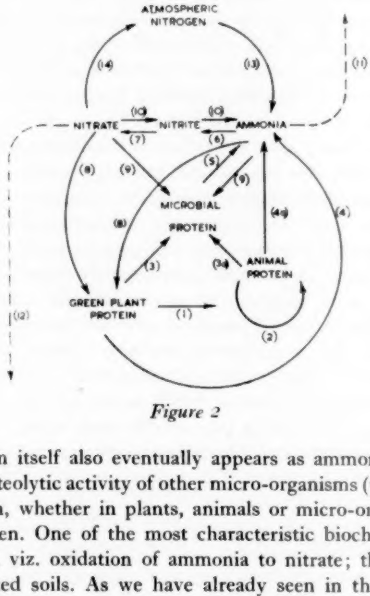

Figure 2

Microbial protein itself also eventually appears as ammonia, as a result of autolysis or the proteolytic activity of other micro-organisms (path 5). Eventually, all protein nitrogen, whether in plants, animals or micro-organisms, reappears as ammonia nitrogen. One of the most characteristic biochemical activities of soil is nitrification, viz. oxidation of ammonia to nitrate; this reaction is very rapid in well aerated soils. As we have already seen in the first lecture, this proceeds through two steps: oxidation of ammonia to nitrite by such bacteria as species of *Nitrosomonas* and *Nitrosococcus* and oxidation of nitrite to nitrate by *Nitrobacter* (paths 6 and 7). The nitrate and ammonia thus formed in the soil are utilized by green plants to form protein, and so the cycle is complete (path 8). However, further details have to be added. Some of the ammonia and nitrate nitrogen is directly assimilated by micro-organisms (path 9). There are many micro-organisms, especially bacteria, capable of reducing nitrate to ammonia *via* nitrite (path 10), but this reverse process seldom outweighs the nitrification process; in waterlogged soils it may become significant, even dominant. This

would appear at first sight to account for all changes in nitrogen. But certain losses from the nitrogen cycle are always taking place—some ammonia nitrogen is lost by volatilization (path 11) and much nitrate nitrogen is lost by leaching (path 12) down to depths of soil where it cannot be reached by plant roots. How is the nitrogen level of soil maintained or actually increased under natural conditions? This problem caused much speculation until it was found, as I mentioned in my last lecture, that certain micro-organisms are capable of fixing atmospheric nitrogen (path 13). This is a process of great significance. It has been estimated that, in 1930, 16 million tons of nitrogen were added to soils in the United States; of this, 6 million tons was in the form of manures and fertilizers and no less than 10 million tons was provided by biological nitrogen fixation. As I explained before, this takes place in the root nodules of leguminous plants (symbiotic nitrogen fixation) and in the soil as a result of the activity of free-living organisms. Symbiotic nitrogen fixation appears to be the more important; the nitrogen increases taking place in a lucerne crop have been estimated to be of the order of 250 lbs. of nitrogen per acre per year, whereas non-symbiotic fixation appears only to be of the order of 25–50 lbs. of nitrogen per acre per year. A certain amount of denitrification (path 14) also takes place as a result of microbiological activity but this is rarely of anything approaching the same order of magnitude as nitrogen fixation.

This may appear a somewhat elaborate set of relationships; actually I have somewhat simplified the picture by omission of some minor reactions. (I have ignored, for instance, that other organic nitrogen compounds besides proteins are involved: protein is quantitatively and qualitatively the most important.) Nevertheless, it is clear that this flow of nitrogen, on which the fertility of the land depends, is largely the result of microbial activity. If it were not for the activity of micro-organisms, the protein nitrogen of animals and plants would only exceedingly slowly become available again for new generations of plants and animals, and if it were not for nitrogen fixation by Bacteria and Blue-Green Algæ, all soils would long since have become completely barren.

A quite similar nitrogen cycle takes place in the sea and in freshwater lakes, though here the only important forms of protein to be considered are microbial and animal, since the main source of plant protein is that formed by microscopic Algæ. The nitrogen cycle in the sea differs only in detail from that in fertile soils. In a fertile soil carrying a crop there are usually appreciable nitrogen reserves even when the crop reaches its highest level of growth. In the sea, however, the supply of nitrogen (and phosphate) limits the amount of production of living matter. Measurements made in the English Channel have shown that in midsummer, when the population of diatoms reaches its highest level, *all* free nitrate and ammonia nitrogen have disappeared from the water and only reappear in the winter, as the diatoms die off. Thus there are alternating peaks of inorganic nitrogen and protein nitrogen; in the soil the peaks are much less marked.

It is possible to make a rough estimate of the total nitrogen in the nitrogen cycle of sea and land. Something of the order of 5,000 million tons of nitrogen

are involved. Most of this is in the oceanic cycle. It is instructive to consider how much of this total nitrogen appears as human protein nitrogen. I estimate it to be something of the order of 2·5 million tons. Thus only a very small fraction of the nitrogen-cycle nitrogen enters into human protein. Feeding a rapidly growing world-population, seen from this angle, only involves diverting a little more of the total nitrogen into the human protein channel.

This completes my very superficial survey of the part played by micro-organisms in the cycles of carbon and nitrogen, which may justly be considered to be basic to all life in the world. Our detailed knowledge of these cycles has been acquired during the last hundred years. It is remarkable, therefore, to find that almost three centuries ago, by some process which must have been largely intuitive, the German alchemist Johan Rudolph Glauber arrived at a fairly accurate conception of the nitrogen cycle. In 1656 he wrote—"The essence of saltpetre (nitrum) is like a wingless bird that flies by day and by night without rest; it penetrates between all the elements and carries with it the spirit of life. . . . From nitrum are originated minerals, plants and animals. This essence never perishes; it only changes its form; it enters the bodies of animals in the form of food and then is excreted. It is thus returned to the soil, from which it again rises into the air with vapours, and hence it is again among the elements. It exists in the roots of plants and in foodstuffs. In such manner the cycle proceeds from the elements to foodstuffs, from food to excrement, and again to elements." The great contribution of the microbiologists and agricultural chemists of the nineteenth century was to explain Glauber's "wingless bird" in terms of the metabolic activity of micro-organisms.

The carbon and nitrogen cycles are not the only chemical cycles in nature which depend largely on micro-organisms. There is, for instance, a sulphur cycle built up of alternating phases of oxidation and reduction. We have already considered several types of sulphur oxidizing organism which oxidize sulphide to sulphur or sulphate. There are also Bacteria capable of reducing sulphate to sulphide, thus completing the cycle. I shall have occasion to mention these again later.

I should like now to approach in a rather different way the interrelationships between micro-organisms and higher plants, by describing two rather special kinds of association. The first of these is the association between micro-organisms and plant roots known as the rhizosphere. Micro-organisms, particularly Bacteria and Fungi (and probably also Protozoa, though I have seen no data on this point), are much more abundant in the immediate vicinity of plant roots than in the soil more distant from the roots. Moreover, in addition to being quantitatively different, the rhizosphere Bacteria are qualitatively different, species dominant in the rhizosphere being relatively much less important in the soil more distant from the root. The nutritional requirements of rhizosphere Bacteria are different from those living free in the soil. There is, then, a specialized zone of microbiological activity around all roots growing in soil. While its existence is well-established, the reason for its existence and its significance to the plant are still to a great extent matters of conjecture. However, it appears likely that,

on the one hand, leakage of materials from plant roots (amino-acids and vitamins are known to leak out of roots at times) will encourage a special root-surface microflora and that, on the other hand, metabolic activities of this concentration of micro-organisms so near to the root must have an effect on the plant. It has been suggested that complex metabolites of the rhizosphere microflora, such as amino-acids, vitamins and antibiotics, will pass into plant roots and affect growth of the plant. Evidence on this point is still scanty. The significance of the rhizosphere to the plant is more clearly established in relation to the economy of inorganic nutrients utilized both by the micro-organisms and by the plant.

Gerretsen, for instance, has shown convincingly that certain insoluble forms of phosphate, not available to plants grown in sterile sand, are solubilized in soil by the rhizosphere microflora and thus made available to the plant. In such a case, the rhizosphere microflora is beneficial. In the case of nutrients in short supply, needed by both micro-organisms and higher plants, the rhizosphere microflora may take all available supplies and deny them to the root. This is particularly well shown in several cases of iron and manganese deficiencies of crop plants. As an example I will mention the "frenching" disease of tobacco. Diseased plants have narrow, strap-like leaves; stem extension is inhibited, so that affected plants remain in the immature rosette form. It can be cured by applications of iron salts to the soil, by sterilization of the soil, or by lowering the soil temperature. At high soil temperatures certain elements of the soil microflora, particularly of the rhizosphere microflora, can and do compete successfully with the plant roots for the available supply of iron. Thus, by providing sufficient iron for both roots and micro-organisms, or by removing the micro-organisms by sterilization of the soil, or by reducing the metabolic activity of the micro-organisms by lowering the soil temperature, iron can be made available for the plant and disease is cured.

The point I want to make is that the classical botanical conception of a root absorbing mineral salts from a biologically inert soil is quite incorrect. The micro-organisms of the rhizosphere act as important intermediaries in the interchange of materials between soil and root and may at times exert a decisive effect.

The second kind of association I wish to mention is an analogous phenomenon in the animal world. Just as the rhizosphere is an association of micro-organisms with the main absorbing surface of the plant, there is to be found a special microflora and microfauna in the gut of many higher animals, again an association of micro-organisms with the main absorbing surface of the larger organism. Among mammals this assumes its most specialized development in the rumen of such ruminants as cows and sheep. Here a specialized association of Bacteria, yeasts and Protozoa acts as an intermediary between the animal itself and the ingested food. On the one hand the micro-organisms may increase the availability of the food. A high proportion of the food ingested by ruminants is carbohydrate in the form of cellulose. Cellulose is not digested in the unaided mammalian digestive tract. In the rumen a vigorous fermentation of the ingested food, in the course of which such unusual end-products as methane and hydrogen are freely produced, leads to breakdown of a considerable part of cellulose to

simpler molecules, notably fatty acids, part of which may be absorbed and assimilated by the animal directly and part after reconstitution in available carbohydrates in the micro-organisms themselves. There are also strong reasons for supposing that microbial activity in the gut may result in the synthesis of vitamins essential to the animal but not initially present in the food. It is possible to induce vitamin deficiency in some animals by administering sulphonamide drugs by the mouth; this result, somewhat surprising at first sight, is the result of inducing changes in the microflora of the gut. The activities of the gut microflora may, on the other hand, at times be disadvantageous to the animal as, for instance, when protein food is degraded with the evolution of ammonia some of which may escape assimilation by micro-organisms and so be lost to the animal.

Similar associations are encountered in insects. Cellulose is made available to many leaf-cutting insects as a result of microbial activity in the gut. Several cases are known of insects depending for their vitamin supplies on microbial activity in the gut and cases are known where, as a consequence, full development from larval to mature stages is not possible in insects reared specially without their normal gut microflora.

In animals, therefore, as well as in plants, micro-organisms can and do act as important nutritional intermediaries, living in an intimate association with the main food-absorbing surfaces.

My next theme, to which I shall devote almost all my remaining time to-day, concerns the relations between soil micro-organisms and certain kinds of plant disease. Of the various kinds of plant disease, among the most important are soil-borne diseases. They are for the most part fungal diseases; a parasitic fungus invades the root and the base of the stem of the host plant and then penetrates the tissues of the plant to a greater or less extent. These diseases vary in scope from damping-off of seedlings in seed-boxes under glass to such diseases as the Panama disease of bananas, which has had such devastating effects on the banana growing industry in the Caribbean zone. Many of these are what are called wilt-diseases; in these the invading fungus secretes certain toxins which travel to distant parts of the plant and induce pathological changes characteristic of the disease. Biochemical investigation of these phytotoxins is just beginning and may in due course lead to new methods of controlling these diseases. But although this is a subject which interests me personally it is not one I wish to pursue this evening. The problem I want to consider is what happens to the pathogenic fungus when the host plant dies.

Let us take as an example the various root- and foot-rots of cereals caused by Fungi of the genera *Fusarium*, *Helminthosporium* and *Ophiobolus*. At the end of the growing season the pathogens remain in the stubble, which eventually is ploughed-in. If another cereal crop is then sown, the pathogens remaining in the infected stubble are able to reinfect the new crop and if cereal crops are sown in several succeeding years the infection builds up and becomes progressively more and more serious. If the cropping sequence is broken for one or more years the infection tends to die out; hence the value of crop rotation in controlling soil borne plant disease.

Why does the infection die out? It is not because soil fails to provide the necessary nutrients for growth of the pathogenic fungus. Species of ***Fusarium***, ***Helminthosporim*** and ***Ophiobolus*** will grow vigorously and perpetuate themselves on sterilized soil. But in natural soil they die out, as a consequence of competition with the normal saprophytic soil microflora. Whereas the many different kinds of "normal" soil micro-organism can live together in association, reaching a dynamic equilibrium with one another, the root-parasites appear to have become somewhat specialized in their habitat requirements and while they can flourish in their own specialized and sheltered habitat, the plant root, they find themselves at a disadvantage in competition with the normal flora of the soil.

Not only is the time during which the pathogens survive in the soil reduced by the saprophytic soil-microflora but the vigour with which they invade host plants is reduced. This can be demonstrated by a very simple experiment. A quantity of uninfected soil is taken and divided into two portions. One portion is sterilized by heat. To both portions is now added an inoculum of a cereal root-attacking fungus and seeds of the cereal sown in both. In the sterile soil infection of the seedlings will be severe, in the other it will be much reduced.

There is, then, an antagonism between the root-parasites and the saprophytic soil micro-organisms. What is the basis of this antagonism? Several explanations have been advanced and there is probably an element of truth in all of them. Until recently the most favoured explanation was based on competition for nutrients—it was suggested that the soil saprophytes were more efficient in mopping-up nutrients in short supply. This may well be an important factor, but there is considerable evidence that other mechanisms are also involved, and it is one of these other suggested mechanisms that I want to discuss.

This phenomenon of antagonism between soil saprophytes and root-parasites is a general one, and plant pathologists concerned with a variety of diseases have investigated it. One obvious line of enquiry has been to determine whether any particular species can be singled out as particularly effective "antagonists". There appears to be an area of fairly general agreement on this point. A number of bacteria, particularly ærobic spore-forming species of the genus ***Bacillus*** and species of ***Pseudomonas***, are effective. Most of the soil Actinomycetes are effective. A number of soil Fungi, especially species of ***Penicillium*** and the ubiquitous soil fungus ***Trichoderma viride***, are effective. There seems little reason to believe that these are the organisms which are most vigorous in the search for food. Have they any other significant properties in common? That question can best be answered after briefly describing an actual research, one that may be regarded as classical.

In the early 1930's an American plant pathologist, Richard Weindling, was working in Florida on a damping-off disease of citrus seedlings. He found that the aggressiveness of the pathogen—in this case a fungus named ***Rhizoctonia solani***—was reduced by the saprophytic soil microflora, and he singled out the mould ***Trichoderma viride*** as especially significant in this respect. He studied the behaviour of the two Fungi when grown together on various substrata and noted that to a certain extent ***Trichoderma*** was parasitic on the pathogen. He

also made the rather surprising and highly significant observation that the *Trichoderma* appeared to be able to kill the pathogen at a distance, without any physical contact taking place.

Such an effect might be produced in various ways; Weindling considered the most likely would be diffusion of some toxic substance from the *Trichoderma*. Following this possibility up, he found that if *Trichoderma* was grown on a suitable liquid nutrient, after some days the liquid medium became highly toxic to the pathogen. He eventually succeeded in isolating this "lethal principle" in pure form. It turned out to be a complex organic material, containing carbon, hydrogen, oxygen, nitrogen and sulphur, with marked fungicidal properties. He named it gliotoxin. He suggested, on this basis, that the antagonistic power of *Trichoderma* in soil was associated with this capacity to produce a diffusible toxin. He was never able to provide unequivocal evidence that this was so. However, the fact that *Trichoderma* was an effective antagonist only in acid soils, although it grew vigorously in neutral or alkaline soils, could be well explained by the fact that the gliotoxin was only stable under acid conditions. I think it most likely that his explanation was correct.

Now you will already have realized that gliotoxin is what we nowadays call an antibiotic. It is of no importance in medicine because, like most antibiotics, it is generally toxic. Moreover those other organisms which I mentioned as particularly good antagonists—Actinomycetes, ærobic spore-forming *Bacilli*, *Pseudomonas* and moulds of the genus *Penicillium*—are all well known now to be active producers of antibiotics. There is, therefore, good reason to believe that production of antibiotics by micro-organisms is not merely a lucky accident for human medicine but is also of considerable natural significance.

I should not like to leave the impression that this suggestion has yet been definitely proved, though the circumstancial evidence in its favour is very strong. One factor of importance that is involved is that for production of an antibiotic a fairly high level of carbon nutrition is necessary; the production of antibiotics in soil under natural conditions would therefore be restricted to certain limited areas such as the vicinity of decomposable organic matter, fragments of plant material or the like, or the rhizosphere. Another factor is that production of an antibiotic by any one species appears to be affected by the other species present in a mixed association of species; in other words there is antagonism between antagonists. However, a recognizable antibiotic—that same gliotoxin discovered by Weindling—has very recently been shown by my colleague Miss Wright to be produced in detectable quantities in a soil containing its normal mixed microflora and microfauna. Thus, evidence is accumulating that this very important antagonism between the saprophytic soil microflora and root-pathogens is associated with the capacity possessed by some micro-organisms for synthesizing substances toxic to other micro-organisms; the fact that metabolites tend to diffuse out of the microbial cell, which I mentioned in my last lecture, gives the capacity for such syntheses extra biological significance.

It should not be thought that this phenomenon of antagonism or antibiosis

is a matter of concern to plant pathology and agriculture only. Many Bacteria capable of causing disease in man and animals, notably some of the less specialized parasites causing intestinal disease, are potentially capable of living and multiplying in soil, but they too tend to die out rapidly as a result of similar antagonisms.

In my first lecture I put forward the view that the main primary habitats of micro-organisms are soil and water. For that reason, and also, I must admit, because it is with organisms of those main habitats that I am most familiar, I have devoted most of my time to-day to them. By doing so I do not think I have been guilty of any serious unbalance and it is true that the significance of free-living micro-organisms is frequently underestimated. However, before concluding this lecture, I must mention the tendency to parasitism which has developed in all groups of micro-organism. The tendency has been least marked, as one might perhaps expect, in those groups entirely independent of organic carbon, viz. the Green Algæ and Blue-Green Algæ. Among Bacteria, Fungi and Protozoa, however, the development has gone far; in each group parasites of the most highly specialized character are known. Though the number of species involved as pathogens is very small as compared to the number of free-living species, the consequence of the activity of these parasites, whether on man, animals or plants, are very great indeed. They have been studied much more intensively than the free-living micro-organisms. Had I been qualified to do so, and had I decided to confine my remarks to these groups of parasites, I could have very adequately filled the whole time at my disposal.

I hope that I have been able to give you an impression that the living processes of micro-organisms and those of the larger plants and animals with which we are more familiar, and indeed our own living processes, are all inextricably bound together in innumerable ways. The fertility of the soil from which we draw our food, the health of the plants and animals we rear on the soil, the workings of our own bodies, are all in some degree dependent on or related to microbial activity. The world of micro-organisms may be unseen, but it is all-pervading.

In his development from the palæolithic savage, man has progressed by increasing knowledge of and control over nature. Though he was unaware until very recently of the existence and physical nature of micro-organisms, he was aware of microbiological activity at a very early stage in his history. As with other natural processes, he very quickly bent microbiological activities to his own needs. This process of harnessing micro-organisms, naturally enough, developed more rapidly as knowledge of micro-organisms developed, and is developing more rapidly to-day than ever before. Great industries are now based on micro-organisms; new microbiological industries are certain to develop. I shall devote most of my next lecture to a consideration of the industrial aspects of microbiology.

III. INDUSTRIAL MICROBIOLOGY

Monday, 1st December, 1952

I want to devote a considerable part of my time to-day to a general discussion of applications of microbiology to industry. I have little special knowledge myself of the details of any industrial fermentation so I shall have perforce to be general in my approach, but in any case I think such an approach will probably be most appropriate to the occasion. In preparing this lecture I have drawn quite heavily in places on material presented by Professor Kluyver, of the Delft Technical High School, in a recent lecture in this country, and I should like to express my indebtedness.

At the end of my last lecture, I mentioned that man made use of microbiological processes long before he had any idea of the nature or even the existence of micro-organisms. It is convenient to begin by consideration of some of these first discovered uses. The food industry has a longer microbiological history than any industry other than agriculture. Bread and cheese and beer are all produced by microbiological processes, whose origins probably go back to neolithic times. The first bread baked by man was probably made by mixing crushed grains with sufficient water to make a sticky dough, followed by baking. It was probably soon found that if the dough were left standing a little while changes took place which resulted in the production of a lighter, better flavoured and more digestible bread. It was later found that if a little dough were saved from each baking and used to inoculate the dough for the next baking, these desirable changes took place more regularly and quickly.

Nowadays, instead of relying on appropriate micro-organisms being present in the flour or on the cooking utensils, the dough is inoculated with a pure culture of baker's yeast—*Saccharomyces cerevise*æ. Enormous quantities of baker's yeast are prepared for this purpose and this itself is probably the largest-scale production of micro-organisms carried out industrially. Once incorporated in the dough, the metabolic activity of the yeast starts off a complex series of changes. Starch is partially broken down to simpler polysaccharides and sugars, thus affecting the flavour. Production of carbon dioxide in respiration of the yeast makes the dough rise so that a bread of light texture is produced. These changes and many others proceed until the temperature in the oven rises sufficiently to kill the yeast and its enzymes. In some countries, particularly of northern Europe, sour breads are appreciated. The panary fermentation involved in the production of these breads is due to a mixed culture containing several acid-producing bacteria. In production of these sour breads, the old custom of saving a little dough from one baking, to inoculate the dough for the next, is still used.

In cheese-making, the whole ripening process is microbiological. Bacteria, yeasts and filamentous Fungi (notably *Penicillium roqueforti* in all the blue cheeses) are involved in a complex fermentation. The starting material for all cheese is

milk—cow's, sheep's, goat's or horse's milk. From this limited range of starting materials a great number of different kinds of cheese can be prepared, of varying *nuances* of texture and flavour; the variety of end-products is to a great extent a reflection of the varying fermentations involved.

Next there is the brewing industry. The principal stages in the process of brewing—malting the grain, mashing, and fermenting the wort with yeast—are basically the same in a modern brewery as they were in breweries hundreds of years ago. But scientific investigation of every step has made it possible to keep up a much higher standard of quality than was possible before the microbiology of fermentation was understood. It is of interest here to recall, parenthetically, the close connection the brewing industry has always had with microbiological research. Pasteur's interests in microbiology arose at least partly from an interest in the technology of brewing, and the famous Carlsberg brewery in Copenhagen supports one of the most famous microbiological research laboratories in the world.

These three examples of the application of microbiology in the preparation of foodstuffs—and these are only examples of a great number of food fermentations, which include such unexpected processes as the production of the tea and cocoa of commerce—may be considered to illustrate the most primitive method, using the word primitive in an evolutionary sense, of the application of microbiology to the service of man. In each of these cases the fermentation has not more than partially changed the chemical nature of the unfermented starting material. The actual food value of the product is not much changed by fermentation, except perhaps in so far as important vitamins and growth factors may be synthesized during the fermentation. The real value of such fermentations as these is in the improvement in gastronomic quality that is achieved. The factors that distinguish a Brie cheese from "ration cheese," or a Mouton-Rothschild claret from a "ruby wine," may be in a material sense very small, but on other scales of value they are very great indeed. It is precisely this kind of improvement of the quality of food that would be so difficult to achieve by synthetic chemistry. As Professor Kluyver recently said, it might eventually be possible to produce synthetically a tolerable gin, but it is exceedingly improbable that one could produce a *vin de château* by such means.

Before leaving the subject of food, another aspect of the relation of microbiology to industry may be mentioned. That is that while micro-organisms can be of the greatest value in the preparation of food, they can also be the cause of much wastage of food. The development of urban civilization has resulted in the necessity for storing considerable bulks of foods of all kinds. These stockpiles, naturally enough, form ideal breeding grounds for micro-organisms, and highly significant quantities of food are lost annually in this way. Prevention of such losses in store has necessitated considerable research programmes in most countries and the problems are by no means overcome yet. Not only food is destroyed by microbial activity. Experience of the armed forces in the Far East during the last war showed that almost all organic materials, from textiles to the cement in camera lenses, are susceptible to microbial attack, unless elaborate

precautions are taken. A weed is a plant in the wrong place; micro-organisms can on occasion be the most pernicious of weeds.

But I want to pass now to a consideration of some more modern productive applications of microbial metabolism. You will recall that in the first lecture I showed how most micro-organisms provide themselves with energy by dissimilation of organic materials. This dissimilation can take the form of oxidative processes involving the intervention of molecular oxygen, or "fermentation" in which molecular oxygen does not intervene. Examples of the former are:

$$C_6H_{12}O_6 + 6O_2 \longrightarrow \underset{\text{Carbon dioxide}}{6CO_2} + 6H_2O$$

$$C_6H_{12}O_6 + 5O_2 \longrightarrow \underset{\text{Oxalic acid}}{2COOH.COOH} + 2CO_2 + 4H_2O$$

$$C_6H_{12}O_6 + 1\tfrac{1}{2}O_2 \longrightarrow \underset{\text{Citric acid}}{COOH.CH_2.\underset{\displaystyle COOH}{\underset{|}{C}}OH.CH_2.COOH} + 2H_2O$$

$$CH_3.CH_2OH + O_2 \longrightarrow \underset{\text{Acetic acid}}{CH_3.COOH} + H_2O$$

and of fermentation:

$$C_6H_{12}O_6 \longrightarrow \underset{\text{Ethyl alcohol}}{2CH_3.CH_2.OH} + 2CO_2$$

$$C_6H_{12}O_6 + H_2O \longrightarrow \underset{\text{Acetone}}{CH_3.CO.CH_3} + 3CO_2 + 4H_2$$

$$C_6H_{12}O_6 \longrightarrow \underset{\text{Lactic acid}}{2CH_3.CHOH.COOH}$$

It will be clear to you that if appropriate micro-organisms could be induced under industrial conditions to carry out these reactions approximately quantitatively, and to deal with adequate quantities of starting materials, economic processes might well be developed. And indeed this has been done in several instances.

I will mention only two examples, the industrial production of citric acid and ethyl alcohol. Until about the end of the First World War, nearly all the world supply of citric acid was obtained from lemons and the industry was mainly centred in Italy. To-day nearly the whole of a much larger world supply is produced by fermentation. The word "fermentation" is used loosely here because the process is highly ærobic. A common mould, *Aspergillus niger*, is grown in large shallow vessels on the surface of a liquid medium containing carbohydrate as molasses. Conversion to citric acid proceeds rapidly and yields of the order of 60 per cent on the sugar consumed are readily obtained; under laboratory conditions much higher yields are possible.

This example may be used to illustrate a characteristic of industrial microbiological processes. Much attention has to be paid, naturally enough, to the

exact composition of the medium, to aeration, to the shape of the vessels in which the fermentation is carried out and to the duration of the fermentation, if maximum yields are to be obtained. But perhaps the most important single factor in the citric acid fermentation, as in all industrial fermentations, is the strain of micro-organism used. Strains of *Aspergillus niger*, very similar if not identical in appearance, vary greatly in biochemical characteristics and may produce very different yields of citric acid. A constant feature of industrial fermentation therefore is a continuous search for new and better strains of the micro-organism being used, and the adoption of special precautions to ensure the maintenance of selected cultures in an active condition. The latter point is of special importance; some micro-organisms seem to maintain their biochemical characteristics well even after prolonged culture, others are very unstable and a system of use of master cultures, which are infrequently subcultured, has to be adopted.

This is perhaps a suitable point to mention a field of microbiological investigation which I have so far not discussed—the genetics of micro-organisms. The instability of strains of micro-organisms has been known for a long time. More recently it has been realized that inheritance and mutation in micro-organisms is a very similar phenomenon to that observed in higher plants and animals and the more rapid multiplication of micro-organisms is now making them more and more popular objects of study by geneticists. Methods of hybridization and breeding of micro-organisms are being developed and there seems to be little doubt that these will lead to much greater efficiency in industrial fermentations of all kinds in the immediate future.

Let us now turn to the production of industrial ethyl alcohol. This is one of the more important starting materials for industrial organic syntheses. Until recently it was all produced by a yeast fermentation similar to that involved in the production of alcoholic beverages, with such materials as molasses as carbon source. But more and more ethanol is being produced synthetically and there seems little doubt that synthetic methods will assume a greater and greater importance in alcohol production. This illustrates a trend that may be of importance in deciding the future development of microbiology in industry. The production of relatively simple carbon compounds, such as ethyl alcohol or citric acid, will always be threatened by synthetic processes based on cheaper starting materials. The cost of production by microbiological means is to a great extent conditioned by the cost of some suitable source of organic carbon, usually carbohydrate, which the micro-organism can use for growth and dissimilation. It seems likely, therefore, that only in special cases and under special economic conditions will micro-biological processes for production of fairly simple carbon compounds be able to survive.

This is certainly not the case, however, with the production of substances of greater chemical complexity, with highly specific properties. I have here in mind such substances as vitamins and antibiotics. The vitamin riboflavin (B_2) is nowadays prepared exclusively by microbiological means. The new and interesting vitamin B_{12}, at first produced with immense trouble and at great cost from liver, will almost certainly soon be produced in quantity from micro-organisms.

The antibiotics, penicillin, streptomycin, aureomycin, terramycin and others are produced microbiologically. These are complex molecules whose relative costliness to produce is no deterrent and which for the most part are quite unamenable to production by purely synthetic means on any scale. An exception is the antibiotic chloramphenicol which was first produced by biosynthesis but is now produced synthetically, but it is an exception. Antibiotic manufacture is a quite new microbiological industry, not more than ten years old, but already one assuming considerable proportions, as the following production figures for the United States (1951) will show:

	Thousands of pounds
Total antibiotics for human or veterinary use ...	1,286
Penicillin salts	625
Streptomycin	39
Dihydrostreptomycin	315

This, I feel sure, is the kind of industrial microbiological process which is likely to expand greatly in the near future.

There is another kind of microbiological synthesis which may well assume some importance. All those so far considered, except those concerned in food preparation, which I mentioned first, really only involve the utilization of by-products of microbial metabolism. Biologically, the most important synthesis taking place in any microbial cell is the synthesis of protein. As we have seen, many micro-organisms can effect this synthesis from very simple starting materials. In view of the world shortage of food, above all of protein, it is natural that the prospects of the use of microbiological protein for food should have been considered. I will mention two possibilities, the use of yeasts and of unicellular Green Algæ.

The production of food yeast was the subject of a lecture to this Society by Dr. A. C. Thaysen in 1945, and I need do little more than recapitulate some of the points he made. Suitable yeasts will grow and multiply in a nutrient medium containing a suitable carbon source, such as molasses, an inorganic source of nitrogen, such as an ammonium salt, and various common mineral salts. From these simple constituents it will synthesize protein amazingly rapidly. Half a ton (the weight of a young bullock) of living yeast will produce, under suitable conditions of nutrition, 245 tons of protein in 24 hours. A bullock of the same initial weight will not produce more than 2 lbs. of meat in 24 hours, containing some 20 per cent of protein. Thus the yeast is far more efficient at protein synthesis. There is little doubt that where suitable carbohydrates are readily available, production of yeast protein would be a most important supplement to the diet of many peoples. There is, of course, a considerable consumer resistance to such unorthodox kinds of food. Everyone, or nearly everyone, would prefer a beefsteak. But is there really any prospect that the choice will be a real one for many of us? Production of food yeast has not gone ahead as rapidly as was expected, largely because otherwise unwanted supplies of fermentable carbohydrate are not as large as was expected. This difficulty leads us

conveniently to consider instead cultivation of a Green Alga. From a theoretical point of view, the possibility of growing a Green Alga on a commercial scale is even more attractive than yeast cultivation. In this case no organic carbon would have to be supplied, since carbon dioxide would be fixed by photosynthesis; all the starting materials needed would be water, a few cheap mineral salts, light, which might be natural or artificial, and possibly an additional supply of carbon dioxide to supplement that present in the atmosphere. Pilot scale experiments have been reported from the United States, using unicellular Algæ of the genera *Chlorella* and *Scenedesmus*. It appears that much more efficient use of radiant energy can be achieved than has yet been found possible in more conventional kinds of agriculture and consequently much greater yields of protein, fat and carbohydrate per acre could be achieved. It may well be, as N. W. Pirie has recently pointed out, that this greater efficiency may be in part due to the fact that the *Chlorella* has been pampered in these experiments far more than conventional crop plants have ever been pampered. Even taking this into account it is likely that the synthesis carried out by the Alga is more efficient, since the whole organism is involved in photosynthesis, whereas the aerial parts of a land plant have to maintain very considerable quantities of root tissue, which live, as it were, parasitically on the aerial photosynthetic apparatus. Not enough is yet known of the economics of large-scale culture of Algæ and all that can safely be said is that it is an intriguing possibility which well deserves further investigation.

Microbiological processes may even be adapted to carry out inorganic chemical reactions of importance to industry. I have time for only one example. You will recall that there are bacteria which will reduce sulphate to sulphide, and others which will oxidize this sulphide to sulphur or sulphate. It might be thought that such processes as these are of academic interest only. This is not so. We owe our knowledge of the actual and potential importance of these organisms largely to a group of workers at the Chemical Research Laboratory, Teddington. They showed some years ago that the corrosion of underground iron pipes is in many cases almost entirely due to the activities of sulphate-reducing bacteria. Corrosion of metals is an electro-chemical process. The corrosion takes place as a result of solution of the metal at the anodes of localized cells set up on the surface of the metal when in contact with salt solutions; these electro-chemical cells are a result of chemical heterogeneity of the metal surface. Under acid, aerated conditions, the process proceeds rapidly. But under neutral conditions, if free access of oxygen is prevented, hydrogen accumulates at the cathodic areas, the electro-chemical cells become polarized and corrosion ceases. In a sterile neutral clay soil, then, corrosion is minimal. But in practice it is in neutral clay soils, under anærobic conditions, that most severe corrosion takes place. It has been shown that this is due to the presence of sulphate-reducing Bacteria and sulphates; under such conditions the Bacteria are able to catalyze the reduction of sulphate by the cathodic hydrogen. This removal of hydrogen at the cathodes prevents polarization and corrosion proceeds and is, indeed, assisted by the sulphides released in the vicinity of the metal surface.

This kind of activity is analogous to the spoilage of food by micro-organisms. Can the sulphur Bacteria be put to some useful purpose? Recent observations by Mr. Butlin and Dr. Postgate, of the Chemical Research Laboratory, suggest that they possibly can. There are a number of lakes in the desert of Cyrenaica. The water they contain, like most desert waters, is highly saline, containing, among other salts, considerable quantities of calcium sulphate. Deposits of sulphur accumulate in these lakes and collection and drying of this sulphur form the basis of a small local industry. One lake containing about 500,000 gallons of water produces 100 tons of sulphur annually.

Butlin and Postgate have examined these lakes and have found that the basis of the sulphur production is microbiological. A heavy population of anærobic sulphate-reducing Bacteria reduce the dissolved calcium sulphate, releasing sulphide as hydrogen sulphide. On the mud around the edges of the lake is a heavy population of green and purple photosynthetic sulphur Bacteria which oxidize the sulphide to sulphur by the mechanism we discussed in the first lecture. The green sulphur bacteria, which deposit the sulphur outside the cell, are apparently more important than the red sulphur bacteria. Thus this symbiosis between sulphate-reducers and photosynthetic sulphur oxidizers leads to production of elemental sulphur from sulphate in quite large quantities. Butlin and Postgate have suggested that, in view of the shortage of sulphur in this country, of which we heard much some months ago, it might be worth investigating this process further. Production in these desert lakes might well be increased by adding waste organic material; addition of organic matter is known to increase sulphate reduction. The whole cycle might be carried out under industrial conditions, but it is not possible yet to say whether this would be an economic proposition. It seems a little strange at first sight to consider production of such a substance as sulphur microbiologically. However, it is not so unnatural as it seems. There is very good reason for believing that the extensive sulphur deposits of Texas and Sicily were originally produced microbiologically in shallow seas, which have since dried up, the sulphur becoming as it were fossilized. It might well be worth while, even from the industrial point of view, to investigate the inorganic chemistry of micro-organisms a little more closely.

Before finally leaving the subject of industrial microbiology, I have one more comment to make. The greatly intensified interest in industrial fermentations during the last decade, particularly in the antibiotic fermentations, where it is of critical importance to prevent the development of contaminant micro-organisms in large fermentation-vessels, has led to a new kind of engineering—microbiological engineering. A modern penicillin plant is a most complex piece of apparatus and one highly surprising to many mycologists. The mycologist has traditionally grown his moulds on the surface of solid or sometimes liquid media. In the penicillin plant, the mould which produces the antibiotic—*Penicillium notatum*—is grown in deep tanks, vigorously agitated, with enormous quantities of sterile air continuously blown through. Mycologists were amazed to find that a mould grew under such conditions; in fact, it usually grows more rapidly. The development of this new kind of engineering, which is at present

still in its infancy, will not only revolutionize prospects of the adoption of microbiological processes in industry but will also have its effect on the design of laboratory apparatus and so have its effect on the acquisition of fundamental knowledge of microbial life processes. This can be seen happening to-day.

With that, I must conclude my brief survey of the significance of microbiology to industry. I hope I have reminded you of many of the existing microbiological industries and given you some hint of what may be coming. I want now, in conclusion, to try to make some general assessment of the status of microbiology as a branch of science.

Perhaps it would be best if I were to recapitulate briefly what I have tried to tell you in these lectures. There is an unseen world of great numbers of many different kinds of micro-organism, an all-pervading world, interlocked in many ways with the more familiar world of macroscopic plants and animals. This unseen world includes organisms capable, like ourselves, of obtaining the energy on which their life depends, by aerobic oxidation of organic substances, in other words by aerobic respiration. It includes also organisms to whom oxygen means death, organisms able to utilize the radiant energy of the sun in one or more of several distinct ways, and organisms capable of obtaining energy from oxidation of inorganic materials. It includes organisms whose nutrient requirements may be only a few simple mineral salts and carbon dioxide, and organisms with nutritional requirements far more complex than our own. It includes organisms living free in soil and water and organisms which have adopted a highly specialized existence in the bodies of plants and animals. These microscopic organisms play a most important part in maintaining the fertility of sea and land, in assisting the digestive processes of higher animals, and in causing disease in man, animals and plants. There is scarcely any aspect of our life where they do not intervene to some extent. As we have come to understand them more, we have been able to minimize the less desirable ways in which they affect our lives, but by harnessing their remarkably versatile chemical activities industrially we have increased their beneficial effects. We have a long way yet to go along this road.

I think you will agree with me that micro-organisms are well worth study, whether from the point of view of possible industrial applications, or from the point of view of getting a better understanding of the scientific basis of medicine and agriculture, or from the more long-term and fundamental point of view of increasing our understanding of cell physiology and biochemistry, and of genetics. If you are prepared to agree with me on that, I want to carry you a little further and ask you to agree that it is worth studying these things as a whole.

As I have already hinted, the study of microbiology is, in the universities of this country at least, split between different traditional faculties. Algæ and Fungi are studied in botanical departments; Protozoa in zoological departments; Bacteria are nearly always studied in medical faculties. I would be the last to deny the value of associating the study of micro-organisms with general biological study. On the other hand, since in nature the different kinds of micro-organisms exist in mixed communities, since so many of the problems of their existence are related to their size, since the basic metabolic activities in different groups are

so closely related, and since their study involves very similar techniques, whether they are Algæ, Fungi, Protozoa or Bacteria, surely it is logical that general microbiology should be recognized as a distinct branch of science. There is a considerable and growing demand to-day for microbiologists with this general background of knowledge. There are signs of development in the required direction—Chairs of Microbiology are being instituted or considered. But as yet no department or institute exists in this country where general microbiological training and research, of the breadth I have tried to suggest in these lectures, is actually going on. Suitable staff for such an institute could not be conjured up immediately. It would have to start from small beginnings. But I do think, and I hope you will agree with me, that somewhere in this country the attempt should be made.

GENERAL NOTES

TURNER AND GIRTIN

"If Tom had lived I would have starved" is a remark of Turner's at once best known and least explicable to those who admire his lonely genius and remember the prodigious industry and thrift that allowed him to leave £140,000, and to the nation some 19,000 sketches. The present coincidence of a collection of Turner's paintings and water-colours at the Whitechapel Art Gallery, and an exhibition of Tom Girtin's water-colours at Agnew's, Old Bond Street, recalls that admission, and allows us to consider afresh these disparate, but close companions.

The Whitechapel exhibition is particularly valuable in that it illustrates every possible aspect of Turner's development (with the justifiable exception of those mythological compositions that he could turn out all too mechanically) including many of his more enigmatic and unfamiliar pictures. It is curious, for example, to see his attraction to the extravagances of Fuseli in a visionary *Skeleton falling off a Horse in Mid-Air*, and to observe his misunderstanding of both Titian and Rembrandt in an early painting of *The Holy Family*. But if the exhibition contains an unusual number of oddities—and the much patched-up *Jessica* from Petworth is not the least disconcerting of these—it also shows Turner in his serenest mood in the early *Dort Packet-Boat from Rotterdam*, becalmed on its estuary like some sublimated Bonington, and in a fever of inspiration in a miraculous late *Seascape*, lent by Sir Kenneth Clark and publicly shown for the first time. Add *The Evening Star* and the prismatic *Falls of Clyde*, that vision of amber and gold, the great painting of Venice from Lord Grimthorpe's collection and the *Morning after the Wreck* from the National Museum of Wales, and one has skimmed the cream of the canvases here.

As might be expected, it is in his water-colours of all periods that one can best judge the range and scope of Turner's art from his early topographical essays, that reveal the influence of Girtin and J. R. Cozens, to his last sketches when the representation of specific forms had been reduced to a minimum, and the image of an iceberg could be summarized, and dissolved in atmosphere, almost beyond recognition. In fact the most consistent feature of Turner's development, as Sir John Rothenstein has observed, was his "gradual loss of interest in the whole material world and his increasing preoccupation with aerial forms suffused with dazzling light"; and even had Girtin survived well into the nineteenth century, identifying

himself with nature and exploring her appearances still further, it is hard to believe that he could ever have rivalled so singular a phenomenon as Turner, still less surpassed him.

Nevertheless Girtin's impressive powers, limited only by his more restrained and predictable temperament, are well brought out in Agnew's exhibition, illustrating every phase of his development from 1791 to 1802 when he died at the age of twenty-seven. Like Turner (whose reputation, remember, was first established as a water-colourist) Girtin inherited the English topographical tradition, evolving however an entirely personal style in designs of noble simplicity and breadth that are instinct with poetry in such later romantic works as the *Bolton Abbey* here. At the same time the limits of his imagination are clearly marked in *A Subject from Ossian*, a vision of cloud drifting up and swirling round a dark headland whose drama is entirely nullified by the precise notation of the foreground figures where Turner would have adumbrated them.

But if Girtin usually appears most at ease in his landscape prospects of medium size—the structure built up with finely gradated washes, and the detail of some cathedral or castle firmly indicated with a reed pen—it must also be recognized that in such large and substantial pictures as his views of Harewood House he goes beyond the natural limitations of water-colour without the least suggestion of over-straining it. All that we have cause to regret is that the colour has faded appreciably in several instances, chiefly however in the skies, so that the values are not so much falsified as might be feared. Certainly if his drawings have the power to move us now, it is easy to understand how even more inspiring they were to Constable, who acknowledged the debt, to De Wint, and, as we have seen, to Turner in his youth. To the lenders to this valuable exhibition, and chiefly to Mr. Thomas Girtin, the direct descendant of the artist, the thanks of all students of the period are due.

NEVILE WALLIS

WESTMINSTER ABBEY TREASURES EXHIBITION

The Dean and Chapter of Westminster have arranged an exhibition of Westminster Abbey Treasures, which is now being held at St. James's Palace by gracious permission of Her Majesty The Queen, in connection with the appeal for £1,000,000 for urgent repairs at the Abbey. The exhibition includes some of the Abbey's plate, manuscripts, records, frontals, statuary and pictures, and will be open on week-days from 11.30 a.m. to 6 p.m. until March 28th. The admission fee is 2*s*.

NOTES ON BOOKS

ENGLISH DRAWINGS OF THE TENTH AND ELEVENTH CENTURIES. *By Francis Wormald. Faber*, 1952. 30*s*

In this latest of the Faber and Faber monographs concerned with serious art-historical research, Professor Wormald has aimed at giving a short account of the stylistic changes and modifications to which English outline drawing was subjected between the years A.D. 900 and A.D. 1100. The account is, indeed, short and perhaps almost too limited, but the careful analysis of the manuscripts which suit his title makes a considerable advance on previous scrutiny. The author has added a catalogue of manuscripts containing these drawings, 59 in all, without making any claim to completeness, and a useful, pleasurable selection of plates illustrates his commentary.

The essay begins with some pertinent remarks on the distinction between outline drawings, ink or coloured line, and those of a more luxurious character, illuminations in heavy body colour and burnished gold. The important point is that the tradition must have gone back to late antique times, to which the nearest surviving approach is a number of papyrus drawings of the fifth and sixth centuries, and a drawing of

Job and his daughters in a seventh century Coptic MS. at Naples. The Joshua Rotulus, whatever its date may be, bears added witness to this late antique tradition.

The main contribution to learning, however, is made by a distinction between two styles in English outline drawing: the first style, which derives from the "Ada" School of Carolingian illumination, is exemplified by the drawing of St. Dunstan prostrate before Christ [Oxford: Bodl. M.S. Auct. F. iv. 32, fol. 1]; the second style, which depends on the Rheims School, is clearly influenced by such manuscripts as the Utrecht Psalter. The first style seems to be the earlier of the two, but having made the distinction, Professor Wormald is careful to avoid the danger of over-simplification and admits that already in the last quarter of the tenth century there are signs of the combination of the two styles.

Perhaps rather less convincing is the section dealing with the effect of Viking taste on the English scriptoria. At least one Scandinavian scholar seems reluctant to accept the burden of Viking taste and prefers to see it as an English manifestation with repercussions in Scandinavia. Dr. Holmqvist, in an important publication in *Acta archæologica*, Vol. 22 (1951), suggests that the origins of Viking tastes are to be sought in England rather than in Scandinavia, and denies to the latter any style-creating role in art.

The whole course of the eleventh century seems, at the present stage of our knowledge, flagged with question marks. The problems of Norman and English spheres of influence become increasingly important and difficult to resolve, when so much of the material from the Norman scriptoria remains still unpublished. It seems clear that a "Winchester" style was current on both sides of the Channel. Can one be sure that all the manuscripts catalogued here originated in fact in English scriptoria? The presence of the Abbot of Fleury in England is mentioned on p. 33, but the influence that this monastic centre may have had is not otherwise considered.

Furthermore, there is the problem of the influence of Ottonian Schools. It seems difficult to believe that there was no close contact between the English schools and those of West Germany and the Rhineland. Cnut's journey to Rome in 1027 to attend the coronation of the Emperor Conrad must have resulted in more than political and economic concessions. If England had relapsed into something approaching isolation in the later years of Æthelred II, Cnut was only too eager to open up diplomatic negotiations with the sovereigns of Europe and in those days such negotiations were usually accompanied by works of art. Admittedly, the characteristics of such a manuscript as the Pericope of Henry II do not appear in English art at this time but that is not the whole story. The general hardening of the figure style throughout the century, the solidifying of the form under the drapery, the elongation of the forms, the tendency towards a vertical axis of composition as opposed to the Carolingian horizontal sprawl, the compacting of figure groups into a massed complex would seem to depend on, or be stimulated by, the Ottonian revival. The drawing of the Spirit Brooding on the Waters [Oxford: Bodl. M.S. Junius II, p. 6] illustrated on plate 18, suggests a conception of space which is surely Ottonian.

These reservations and queries, however, must not be considered to detract from a work which contains so much detailed analysis of the stylistic sequences of the tenth and eleventh centuries. It is to be hoped that Professor Wormald will publish more frequently the results of his work in a field where there are still considerable areas to be uncovered and assimilated. For it is from particular monographs such as this that a general understanding of the period will gradually come.

JOHN BECKWITH

NOTE: Copies of the *Graphis Annual* 1952/53, edited by Walter Herdeg and Charles Rosner (63s.) which was reviewed in the *Journal* of 26th December, may be obtained from the Sylvan Press, who are the sole distributors of the *Annual* in Great Britain.

LIBRARY ADDITIONS

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SMITH, ALBERT HUGH. Piers Plowman and the pursuit of poetry: an inaugural lecture delivered at University College, London, 23rd February, 1950. *H. K. Lewis for the College*, 1951.

BIOGRAPHY

FUSSELL, G. E. Impressions of Sir John Sinclair, bart., first president of the Board of Agriculture; reprinted from *Agricultural history*, 25: 162–169. October, 1951.

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FROM THE JOURNAL OF 1853

VOLUME I. *4th March*, 1853

From the Proceedings of Institutions

SOUTHAMPTON.—On Wednesday evening, a Lecture was delivered at the Polytechnic Institution, on "Books", by the Rev. J. W. Wyld. The lecturer carried his audience back to the period when the rude hillock or unsightly stone erections were the unmeaning records of some important event or distinguishing achievement. He then gradually conducted them through the successive eras of literary progress, including the leaf, skin, and manuscript, until the mighty lever of intellectual power —the Printing Press—appeared upon the stage of human enterprise. The secret of success or failure among authors was clearly developed, and a well-timed satirical rebuke levelled against brainless writers and presumptuous pamphleteers. The lecture abounded with interesting literary statistics, beautifully interwoven with originality of thought, great truths, and practical comments; and at its close the lecturer was awarded a cordial vote of thanks by the audience.

Some Meetings of Other Societies

MON. 23 FEB. Electrical Engineers, Institution of, Savoy Place, W.C.2. 5.30 p.m. G. W. Stallibrass : *Radio Aids for Airport Control.*

Geographical Society, Royal, S.W.7. 8.15 p.m. S. M. Manton : *Progress of Soviet Planning in Central Asia.*

Imperial Institute, S.W.7. 5.30 p.m. S. C. Terezopoulos : *The Colonial Empire : Cyprus and the Mediterranean.*

TUES. 24 FEB. Chadwick Trust, at the Royal Society of Tropical Medicine and Hygiene, 26, Portland Place, W.1. 2.30 p.m. Georges Dechameux : *Industrial Medicine and Hygiene in Belgium.*

Manchester Geographical Society, 16, St. Mary's Parsonage, Manchester, 3. 6.30 p.m. Osmund Hood : *Holiday in Austria.*

WED. 25 FEB. British Foundrymen, Institute of, at the Waldorf Hotel, W.C.2. 7.30 p.m. F. C. Evans : *Operating Experiences with Hot Blast Cupolas in Great Britain.*

Electrical Engineers, Institution of, Savoy Place, W.C.2. 5.30 p.m. H. Barker and H. Davies : *The Testing and Specification of Bushings in Relation to Service Conditions.*

Victoria & Albert Museum, S.W.7. 6.15 p.m. Martin Holmes : *The Evolution of the Royal Crown.*

THURS. 26 FEB. Chemical Society, at the Royal Institution, Albemarle Street, W.1. 7.30 p.m. A. Tiselius : *Some Applications of the Separation of Large Molecules and Colloidal Particles.*

Structural Engineers, Institution of, 11, Upper Belgrave Street, S.W.1. 5.55 p.m. P. L. Capper : *Soil Mechanics in Relation to Structural Engineering.*

FRI. 27 FEB. British Sociological Association, at the Royal Society of Arts, W.C.2. 8 p.m. A. King : *Industrial Research and the Social Sciences.*

Mechanical Engineers, Institution of, Storey's Gate, S.W.1. 5.30 p.m. F. Buckley : *Developments in Steel Castings in the Heavy Power Plant Industry.*

SAT. 28 FEB. Horniman Museum, Forest Hill, S.E.23. 3.30 p.m. L. E. Tanner : *Some Aspects of the Coronation Ceremony.*

MON. 2 MAR. Imperial Institute, S.W.7. 5.30 p.m. J. P. Athisayam : *The Colonial Empire : Malaya and Singapore.*

TUES. 3 MAR. British Architects, Royal Institute of, 66, Portland Place, W.1. 6 p.m. Osbert Lancaster : *The Future of the Past : some thoughts on preservation.*

Electrical Engineers, Institution of, Savoy Place, W.C.2. 5.30 p.m. (1) E. H. Frost-Smith : *The Study of a Magnetic Inverter for Amplification of Low-Input-Power D.C. Signals.* (2) P. S. T. Buckerfield : *The Parallel-T D.C. Amplifier : a Low-Drift-Amplifier with Wide Frequency Response.*

Japan Society of London, at the Victoria & Albert Museum, S.W.7. 5.30 p.m. Geoffrey Hudson : *Jimmu Tenno.*

Manchester Geographical Society, 16, St. Mary's Parsonage, Manchester, 3. 6.30 p.m. R. F. Peel : *Mountains of the Moon.*

WED. 4 MAR. British Kinematograph Society, at Film House, Wardour Street, W.1. 7.15 p.m. W. de Lane Lea : *Modern Technique in Post Synchronisation.*

Victoria & Albert Museum, S.W.7. 6.15 p.m. H. D. W. Sitwell : *The Crown Jewels.*

THURS. 5 MAR. Electrical Engineers, Institution of, Savoy Place, W.C.2. 5.30 p.m. S. D. Whetman and A. F. Powell : *Design Features of Certain British Power Stations.*

Engineering Inspection, Institution of, at the Royal Society of Arts, W.C.2. 6 p.m. A. W. Mason : *Manufacture-Inspection and Erection of Oil Refinery Equipment.*

SAT. 7 MAR. Chemical Engineers, Institution of, at the College of Technology, Manchester. 3 p.m. K. Greenwood and M. Pearce : *The Effect of Packing Size on the Absorption of Carbon Dioxide from Air with Caustic Soda Solutions.*

Horniman Museum, Forest Hill, S.E.23. 3.30 p.m. John Layard : *The Journey of the Dead in Malekula, New Hebrides.*

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